Gaia again

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\begin{abstract}

The ideas of the Gaia hypothesis from the 1960s are today largely included in global ecology and Earth system sciences. The interdependence between biosphere, oceans, atmosphere and geosphere is well-established by data from global monitoring. Nevertheless the theory underlying the holistic view of the homeostatic Earth has remained obscure. Here the foundations of Gaia theory are examined from the recent formulation of the 2nd law of thermodynamics as an equation of motion. According to the principle of increasing entropy, all natural processes, animate just as inanimate, consume free energy, the thermodynamic driving force. All species, abiotic just as biotic are viewed as mechanisms of energy transduction for the global system to evolve toward a stationary state in its surroundings. The maximum entropy state displays homeostasis by being stable against internal fluctuations. When surrounding conditions change or when new mechanisms emerge, the global system readjusts its flows of energy to level newly appeared gradients. Thus, the propositions of Gaia theory and holistic understanding of the global system are recognized as consequences of thermodynamic imperatives,

\end{abstract}

\section{Introduction}

The Gaia hypothesis (Lovelock, 1988; Lovelock and Margulis, 1974) by James Lovelock has been a subject of intensive debate. The bold hypothesis proposed that Earth is a giant organism where all living and nonliving entities interact and evolve together to maintain life on the planet. Today Gaia theory is largely recognized as an early vision of modern global ecology that voiced the interdependence between biota, oceans, atmosphere and geosphere. Lovelock was prompted to postulate a global homeostasis by the basic observation that Earth is unique among other planets in our solar system in having an atmosphere that has, for eons, been far from chemical equilibrium (Lovelock, 1972). It appears that all life on Earth regulates the living and nonliving environment so as to keep conditions such as ambient temperature and composition of the atmosphere and oceans suitable for life.

Like-minded views and evidence suggesting that Earth may be regarded as a gigantic organism had been expressed earlier by others (Lovelock, 1988: Kirchner, 2002), but the Gaia hypothesis reached a more wide-spread notoriety and generated a lively discussion about the definition of an organism and life in general. The Gaian ideas have been broken down into several different propositions (Kirchner, 2002; Barlow and Volk, 1992), of which some are perhaps regarded as lofty and ideological, whereas those more precisely formulated have been deemed scientific and testable. The central aspect of all of these is some form of self-regulation or homeostasis of the global system. Specific criticisms against the Gaia hypothesis have focused on the identity and nature of the mechanisms behind the global homeostasis. Indeed it has remained perplexing how global-scale cooperation could evolve from mutual competition that leads to natural selection of the fittest (Lenton, 1998; Barlow and Volk, 1992).

Considering the on-going climate change and other global environmental changes, it is time to inspect Gaia again in the light of the theory of evolution by natural selection (Darwin, 1859) that was recently founded on the thermodynamic principle of increasing entropy (Sharma and Annila, 2007). The fundamental formulation makes no distinction between animate and inanimate, but views all matter in motion as a result of energy transduction to diminish thermodynamic driving forces. Flows of energy channel down the steepest gradients. The thermodynamic imperative has been shown to be equivalent to the principle of least action that directs flows along the shortest paths (Kaila and Annila, 2008). The theoretical formulation has been used to account for the ubiquitous skewed population distributions of plants and animals, as well as genes and their sigmoid cumulative curves (Würtz and Annila, submitted for publication; Grönholm and Annila, 2007). Furthermore, the emergence of chirality consensus and other standards of life have been rationalized (Jaakkola et al., 2008a). The theory also tackles the

\begin{keywords}
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Natural selection
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\end{keywords}
puzzle of large amounts of non-expressed DNA in eukaryotes (Jaakkola et al., 2008b). These recent findings are consistent with the results derived earlier from the maximum entropy principle (Brooks and Wiley, 1988; Lorenz, 2002; Salthe, 1993; Schneider and Kay, 1994; Ulanowicz and Hannon, 1987).

In this study it is clarified that the 2nd law of thermodynamics underlies Gaia theory. Thermodynamics is used to explain the nature and mechanisms of homeostasis in addition to giving definitions for an organism and for life in general.

2. Driving forces and flows

The 2nd law of thermodynamics (Carnot, 1924) was associated with the statistical imperative of increasing entropy by Boltzmann (1886) and of decreasing free energy by Gibbs (1993–1994). In accordance with this physical meaning, the concept of entropy is employed in this study as a measure of energy dispersal that obtains its maximum when all gradients of energy have vanished. To clarify the adopted standpoint, it is noted that the informational entropy defined by Shannon (1948) is not used here because it does not express entropy explicitly in terms of energy. The maximum entropy principle formulated by Jaynes (1957) builds on the theoretical framework used and the results presented here are not new to other compounds.

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hand, when $\nabla T_{ij}/k_B T < 0$, $N_j$ is in for a downsizing one way or the other to benefit other populations $N_k$.

The flow rate $v_j$ is proportional to the mechanistic constant $r_k > 0$. For example, energy may dissipate by a laminar flow or a turbulent transport mechanism. According to the 2nd law a hurricane is a mechanism that develops to funnel heat from tropical seas to the cold troposphere (Emanuel, 1991). Likewise, chemical reaction rates depend on transformation mechanisms such as catalysis. Upon closer examination, every mechanism can be regarded as a system of its own that emerged from an earlier natural process. For example, an organism is an entity of an ecosystem and also a system of its own that is composed of cells that, likewise, are systems of molecules. In other words, the global system has evolved toward increased dispersal of energy as numerous energy transduction systems have integrated into larger and larger systems. The criterion $dS > 0$ (Prigogine, 1961) is the general condition of integration. The energy transduction is self-similar, i.e., a larger system is the surroundings for its subsystems. For example an ecosystem is the surroundings for each organism that in turn is the surroundings for its cells. The scale-independent thermodynamic description of energy transduction is applicable to all levels of hierarchy.

The diverse mechanisms are valued by their rates of entropy increase, i.e., ability to diminish energy gradients. The rate has been recognized also earlier as the fitness criterion (Brooks and Wiley, 1988). Mechanisms that provide fast energy transduction, equivalent to fast rates of entropy increase or to the shortest paths, are favored. They are naturally selected (Sharma and Annila, 2007). Every time a new energy transduction mechanism emerges, evolution is punctuated by a rapid increase in the transduction. Later the natural process settles toward a stasis when the potential difference begins to be exhausted (Eldredge and Gould, 1972; Snoep et al., 1995). The overall course is sigmoid. Initially the thermodynamic gradient is large, but the rate of evolution is limited by the newly emerged mechanistic capacity. When more mechanisms emerge, the flow of energy increases rapidly but later it slows down toward the stasis, being then limited by the nearly depleted gradient. At the stationary state all potential gradients driving changes in populations have vanished. There is no net-flux but through-flux powers numerous motions. A highly effective mechanism may emerge in response to a large potential but it will also require at the stationary state the large potential to supply the vital through-flux.

The characteristic sigmoid course of a natural process that may repeat itself over and over again, is often closely approximated by the biphasic form of the logistic equation (Strogatz, 2000). Also the law of mass action is often a good approximation for the flow equation (Eq. (2)) just as the Onsager reciprocal relations for cross correlated phenomena in the vicinity of the equilibrium and non-equilibrium stationary states (Kondepudi and Prigogine, 1998). Variations in potentials, as well as in mechanistic capacity, may trigger oscillations that are modeled by the Lotka–Volterra equations. Obviously, the varying external flux drives annual and circadian oscillations. However, it is emphasized that these well-known and widely used analytical approximations for the flow equation (Eq. (2)) do not capture the fact that evolution is non-deterministic, i.e., Eq. (1) cannot be solved analytically because flows consume the driving forces that, in turn, direct flows (Sharma and Annila, 2007). The arrow of time (Eddington, 1928), the sense of irreversibility, results from the influx or efflux of energy (Sharma and Annila, 2007). The open system acquires or loses energy. Even a small change in conditions at an early time point will affect the outcome at a later time. Thus, by definition (Strogatz, 2000), natural processes can even be chaotic.

### 3. The system characteristics

According to thermodynamics, all systems at all levels of hierarchy (i.e., molecules, cells, organisms, etc.) are regarded as mechanisms of energy transduction. Obviously the amount of energy that is dissipated when, e.g., a hydrogen bond forms is minute in comparison to the overall energy transduction of an organism. The scale is different, the principle, however, is the same.

Energy transduction systems will respond to internal and external changes by adjusting diverse $m_j$, hence also $N_j$ and $G_j$. Intensive interactions by effective mechanisms lead to a rapid adaptation, i.e., re-dispersal of energy in response to the change in conditions. At the stationary state when all potential gradients $v_{ij}$ are fully and efficiently in use by diverse mechanistic populations $N_j$, the resulting natural distributions of $N_j$ are skewed, resembling log-normal distributions (Grönholm and Annila, 2007).

The maximum entropy non-equilibrium state corresponds to the free energy minimum at the maximum dissipation when the through-flux is at a maximum (Lotka, 1922). Often, an ecosystem at the maximum entropy state houses the highest number of different mechanisms to exhaust all available thermodynamic gradients. However, climax systems may reach the maximum dissipation with fewer highly effective species than were present during an earlier disparity (Gould, 1991). This is consistent with the thermodynamic imperative.

The imperative to equalize energy differences is sufficient to display homeostasis at the thermodynamic stationary state. The steady state, the stasis, is stable against internal fluctuations in the optimal populations $N_j$ according to the Lyapunov stability criterion (Kondepudi and Prigogine, 1998; Strogatz, 2000) $dS(dN_j)<0$. $dS(dN_j)/dt>0$. The homeostasis is a mere result of the quest for diminished gradients by maximal energy transduction to bring the system to the maximum entropy state. The mechanisms of homeostasis are the mechanisms of energy transduction. They are intrinsically interdependent by sharing the common constituents on Earth. In accordance with the postulation by Lovelock, the homeostasis is maintained by automatic and unconscious feedback mechanisms of the biota. Thermodynamics sees no difference between abiotic and biotic and no need for explicit controlled maintenance of a stable state as implied by the text-book definition of homeostasis (Cannon, 1932).

The global system is so large and subject to incessantly changing conditions (due to circadian, annual and solar rhythms, the Earth axis-nutation as well as due to more irregular motions such as plate-tectonics) that it is never quite in the stationary state. When the external flux changes, the system is bound to evolve toward a new, more probable state. Adaptation aims to attain the maximum entropy state with respect to prevailing circumstances. The response to the change in conditions leads to a revised optimal state. Small perturbations lead to small changes and thus the system appears homeostatic (Fig. 1). This is also the essence of Le Chatelier’s principle, i.e., external conditions command the state of chemical equilibrium. A small system, such as a bacterium, possesses few mechanisms of adaptation. The large global ecosystem houses many mechanisms of energy transduction to redirect its flows after changes in the external flux to attain the maximum entropy state. However, changes in conditions may be so dramatic that numerous mechanisms vanish abruptly and the system is not able to retain much of its prior energy transduction before powerful mechanisms have re-emerged. Current human endeavors are powerful energy transduction mechanisms consuming diverse sources of energy. Consequently other mechanistic species are endangered.

The thermodynamic principle is simple. When the energy density of a system differs from that of its surroundings, energy flows to reduce the difference. Often, but mistakenly, an animate entity
is viewed as being higher in energy than its surroundings. This may be true for its immediate surroundings but if this were true for the entire range that the animate entity is able to interact with, it would not find enough resources, i.e., free energy, to continue to exist. The global system has evolved in the quest for a stationary state in its high-energy surroundings provided by the Sun. Mechanisms of energy transduction have emerged from the ingredients present on Earth and evolved over the eons to channel flows down along increasingly steeper gradients. Also within the global system all entities, i.e., subsystems, are in relation to one and other via numerous flows according to Eqs. (1) and (2). Energy gradients power evolution and drive adaptation. This is the physical basis of the Gaia hypothesis.

4. Daisyworld simulation

Lovelock and Watson created the daisyworld simulation in a response to the argument that global homeostasis could only result through premediated conscious cooperation of species (Watson and Lovelock, 1983). The simulation has been important in directing further development of Gaia theory. It shows how a simplified planetary system could unintentionally maintain a surface temperature suitable for its biota when the luminosity of the central star keeps increasing. Earth is clearly more complex than daisyworld, but analogously the output of our Sun has increased by 25% since the beginning of life and yet the surface temperature of Earth has remained rather stable (Newman and Rood, 1977). It is intensively being studied how organisms and the operations of man affect atmospheric composition by excreted substances, and influence temperature, e.g., by the green house effect.

The evolution of a daisyworld was simulated using the principle of increasing entropy given by Eqs. (1) and (2) (Fig. 1). The self-consistent model is simple but it demonstrates that the essential features of Gaia theory are consequences of thermodynamics. The maximum entropy principle has been applied earlier in the context of daisyworld (as reviewed in Wood et al., 2008; Pujol, 2002), but using phenomenological rate equations rather than the fundamental flow equation (Eq. (2)) that is valid also far from equilibrium. Also cellular automata simulation has been used to show emergent self-regulation as a consequence of feedback coupling between life and its environment (Lenton and van Oijen, 2002), however, without establishing its thermodynamic basis. The simple model can be expanded and refined by including more terms in the master equation of evolution (Eq. (1)) and its flow equations (Eq. (2)) to include more mechanisms and to describe them in more detail. However, there is no need to include additional principles, e.g., to simulate Darwinian processes.

The evolution was programmed as a for-loop of time steps. At each step, dark (D) and light (L) daisies were randomly synthesized using Eq. (2) from base constituents in numbers $N_D$ according to a fixed stoichiometry (10:1) with the help of external energy $\Delta Q$. The energy content of daisies was assigned 100 times larger than that of the basic constituents, i.e., $G_D = G_L = 100 G_i$. The rate of synthesis $u_D$ is given by $\exp[(T_r - T_c)/2a^2]$, $A_{D,L} \propto \exp[(T_c - T_r)/2a^2]$ about the set-point $T_c$ of optimal growth was modeled as a Gaussian. The specific form is not important. For example, a quadratic form that has been used earlier yields similar results (Robertson and Robinson, 1998). The standard deviation $\sigma$ defined the ‘zone of life’. Temperature $T$ of the planet was modeled to increase linearly with increasing $\Delta Q$ and with the population difference between $N_D$ and $N_L$.

Earlier, the Stefan radiation law has been used to link the albedos of daisies with solar insolation. Instead the Planck radiation law, which is also a consequence of the principle of increasing entropy leading to the equilibrium between radiation and matter, would be appropriate to model the temperature dependence. However, using the model with only the aforementioned parameters is deliberately simple to demonstrate the principle of decreasing free energy. After each time step, temperature, chemical potentials $\mu_D$, $\mu_L$ and $\mu_i$ as well as the driving forces were updated. Large changes in $\mu_i$ within a step may trigger oscillatory behavior in analogy to chemical oscillations and animal population fluctuations. The fluctuations due to the random variation in syntheses were seen as ‘glacial and warm epochs’.

During the evolution $T$, $N_D$, $N_L$ and entropy $S$ were monitored but not used in any way to direct the course.

The particular choice of parameters corresponds to a specific ‘planet’ and another choice would result in different courses of evolution. Not every ‘planet’ will advance very far by its ingredients but all systems select, from emerging mechanisms, those that provide evolution the fastest rates of entropy increase and are able to maintain the high transduction of energy. In the daisyworld simulation other mechanisms than the dark and light daisies were not allowed to emerge from the random synthesis, however if additional mechanisms were to appear, the energy transduction and entropy would increase further. In this way by evolving mechanisms of energy transduction (Robertson and Robinson, 1998), the system aims at the stationary state in its surroundings. Furthermore, the observed thermostatic behavior (Fig. 1) is not an exclusive property of ‘living’ systems but, e.g., simple physical resonance systems display similar phenomena as well (Oja et al., 1988).

5. Discussion

The thermodynamic account of the homeostatic global behavior provided here is not new as such. The connection between bio-
logical theory and thermodynamics has been established before (e.g., Ulanowicz and Hannon, 1987; Brooks and Wiley, 1988; Collier, 1986; Schneider and Kay, 1994). In particular, the maximum entropy production principle has been used in attempts to understand Gaia theory (as reviewed in Wood et al., 2008; Kleidon, 2004). In general, the maximum entropy production principle is well-recognized as a powerful imperative to understand natural processes. However, it is also instructive to examine natural processes as energy dispersal. Eq. (1) links entropy to energy by identifying entropy increase as the result of flows of energy that decrease differences between thermodynamic potentials. Despite the concise notation, Eq. (1) is not a simplified but an extremely detailed formulation. The summations in Eq. (1) contain every unit of matter and every quantum of energy in the global system, making no distinction between animate and inanimate.

The consilience brought about by the principle of increasing entropy is inspiring. All processes at all length scales have the same motive of energy dispersal (Schneider and Sagan, 2005; Ulanowicz and Hannon, 1987; Brooks and Wiley, 1988; Collier, 1986; Schneider and Kay, 1994; Matsuno and Swenson, 1999). In accordance with Gaia theory and the classic texts of biological physics (Lotka, 1925) and ecology (Lindeman, 1942), thermodynamics makes no demarcation line between the living and nonliving. From the thermodynamic point of view, it is merely our choice to refer to those open systems that have evolved far from equilibrium by external-energy-powered chemical processes, as living organisms. In accordance with earlier thermodynamic argumentation (Lotka, 1925; Maynard Smith and Szathmary, 1995; Brooks, 2001), an organism is an open energy transduction system powered by external flux without further specifications about its mechanisms and modes of energy transduction. Obviously one may introduce further qualifications, e.g., concerning ways of reproduction, to exclude Earth from the definition. The energy gradients experienced by the system direct its evolution. A new mechanism of energy transduction might emerge, e.g., via random variation in the flows within the system or via inflows to the system. Any mechanism that will increase rates of gradient reduction, is naturally selected. Minor improvements direct paths along slightly steeper gradients, major evolutionary transitions open entirely new paths on the free energy landscape. From the thermodynamic viewpoint, life is a natural process powered by external flux without further conditions about its means and mechanisms.

Dissipative structures, i.e., open non-equilibrium systems, may remain stable for long periods of time in a steady stream of external energy. These systems manifest autopoiesis, i.e., they regenerate themselves recursively using the energy and matter flowing through them. The term autopoiesis (Maturana and Varela, 1980), self-production, is often regarded as a general characteristic of living organisms. Genetic mechanisms are highly effective means to instruct the re-emergence of metastable mechanisms to maintain a state of energy transduction, as well as to facilitate the emergence of novel mechanisms (Szathmary and Maynard Smith, 1997) that may eventually attain even higher states of energy transduction. However, it is emphasized that the surrounding densities in energy direct the overall process.

In the context of Gaia theory the term homeostasis is preferably replaced by homoeorhesis (Waddington, 1957, 1968; Margulis, 1990) consisting of piecewise homeostases (Mamontov, 2007). The global system has evolved toward higher energy transduction by punctuations toward states. These episodes have been particularly evident when the global biota has recovered from catastrophes. The trophic hierarchy has reappeared demonstrating that it is the surroundings that direct evolution, but with differing details, exemplifying the non-deterministic nature of evolution (Sharma and Annila, 2007).

The principle of increasing entropy, equivalent to decreasing free energy, is such a strong imperative that it will employ all mechanisms to its end. The non-equilibrium stationary state is attained and maintained by any means, giving the impression of regulation. This statement should not be interpreted to downplay the role of mechanisms. Not every planet contains the suitable mixture of ingredients and bakes in an appropriate energy flux that may couple to the ingredients to come up with an increasing diversity of increasingly more powerful mechanisms over the eons.

In summary, the physical basis of Gaia theory is in thermodynamics of open systems. This is not a new conclusion but is founded on the 2nd law given as an equation of motion. The holistic and scale-independent description of energy transduction, regards both the animate and inanimate as mechanisms to consume free energy. The quest to maintain high dissipation via frequent interactions manifests as homeostasis and adaptation without conscious regulatory mechanisms. The same incentive drives matter during evolution in increasingly more effective mechanisms by naturally selecting those among random variation that provide the highest rates of entropy increase. The global biota emerged over the eons in response to the solar-energy flux, and changed the global climate. Today the global economy is rising in response to the recently accessed contemporary energy supplies and is causing concurrent global changes. We should be thoughtful, in our brief quest for increased entropy by exhausting non-renewable resources, not to damage those vital mechanisms that have cumulated over the eons and would guarantee our existence also in the future (Diamond, 2005).

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